

## THE DIRECTIONAL AND SPECTRAL SENSITIVITIES OF THE RETINAL RODS TO ADAPTING FIELDS OF DIFFERENT WAVE-LENGTHS

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The marked dependence of visual response on the angle at which the rays forming the stimulus strike the retina is believed to be a property of cone vision. When conditions are such that the response to the stimulus is mediated by the retinal rods there is little or no variation with angle of incidence, except possibly for monochromatic stimuli in the orange and red. Experimentally, the angle of incidence is varied by converging the rays from the stimulus to a beam of very small cross-section in the plane of the fully adapted pupil and by directing this beam to different points in the pupil opening. If the same visual effect is produced by beam intensities  $I_c$  and  $I_e$  entering respectively at the centre and near the edge of the pupil, the ratio  $I_e/I_c$  is a convenient measure of the directional sensitivity of the retinal mechanism called into play. Measurements of the threshold intensity  $T$  for a small ( $1^\circ$  square), flashing (0.063 sec. exposure), monochromatic test stimulus seen against a dark background at  $5^\circ$  in the parafovea by the completely dark-adapted eye show that the directional sensitivity  $T_e/T_c$  is nearly constant and equal to unity for wave-lengths  $\lambda$  below about 600 m $\mu$ . but increases to about 4 as  $\lambda$  is increased from 600 to 700 m $\mu$ . (Stiles, 1939). If, in this latter range, the rod mechanism of the retina were solely responsible for threshold vision of the test stimulus for both points of entry—as is certainly the case at shorter wave-lengths—it would be necessary to admit that the response of the parafoveal rods to red light was directional. More probably, however, the sensitivity of the parafoveal cones to a stimulus of the kind used becomes equal to, and then exceeds that of the parafoveal rods as the red end of the spectrum is approached, so that the directional property of the cones may be responsible for the observed directional effect in the red. The possibility of a directional response of the rods to red light would then remain open. In the present work this question is re-examined both by the original method and by a modified method.

The modified or indirect method uses the fact that for a test stimulus of a degree or more in diameter and of short wave-length, say  $490\text{ m}\mu$ ., which is viewed parafoveally, the absolute threshold of the cone mechanism greatly exceeds—by a factor of 100 or more—the absolute threshold of the rod mechanism. This is borne out by the large difference between the achromatic and chromatic threshold, by the high value of the threshold observed a few minutes after intense light adaptation when only the cones have had time to recover (see particularly Wald, 1945), and by the position of the kink corresponding to the rod-cone transition in curves showing the variations of threshold with intensity level (see Stiles, 1939). It follows that if by any means the observed parafoveal threshold is raised above the value for the dark-adapted retina by a factor substantially below 100, then it must still be the rod mechanism which is responsible for vision of the test stimulus at the threshold. Suppose the threshold is raised by exposing the retina continuously to an extended and uniform adapting field of wave-length  $\mu$ , centred on the parafoveal area at which the test stimulus of wave-length  $490\text{ m}\mu$ . is presented. The reciprocal of the intensity of the adapting field expressed in energy units, which is required for different wave-lengths  $\mu$  to increase the threshold above the absolute value by some factor less than 100 defines the sensitivity of the rod-mechanism to the adapting effect of the field. The spectral sensitivity curve found in this way has been shown (Stiles, 1939) to be very similar in shape to that determined by the direct method. Further evidence on this point is given below. If now the *adapting field* is made to enter the eye as a narrow beam, the intensities necessary to raise the threshold by the fixed factor can be determined (*a*) when the beam enters at the centre, (*b*) when it enters near the edge of the dilated pupil, the point of entry of the test stimulus being kept the same throughout. The ratio of these intensities is a measure of the directional sensitivity of the rod mechanism to the adapting effect of light of wave-length  $\mu$ . The advantage of the indirect method of determining the spectral and directional sensitivities of the rod mechanism is that it can be applied throughout the spectrum including the red end, with fair certainty that cone vision is not obscuring the results.

#### METHODS

The apparatus—similar in principle to that used by Stiles (1939) but rebuilt with certain improvements—needs only a brief description. Referring to Fig. 1 (*a*), a parallel beam from a double monochromator (*F*) passes through the lenses  $L_1$  and  $L_2$  which together form a system of zero power, and through the 2 in. beam-splitter cube  $C_1$  to be brought to a focus in the plane of the apparent pupil of the subject's eye *E*, by the lens  $L_3$ . At the focus, the beam forms an image of the exit slit of the monochromator, of height 0.5 mm., width 0.19 mm., and this image can be moved to any position in the pupil, by a motion, in its own plane, of the larger lens of the zero power combination  $L_1L_2$ . The subject sees the lens  $L_3$  as a uniformly illuminated, circular patch of  $10^\circ$  diameter—the adapting field. The test stimulus is obtained in just the same way from a second double monochromator *T*, the patch being limited to a  $1^\circ$  square by the diaphragm  $D_1$  and turned through  $90^\circ$  by reflexion in the beam-splitter cube  $C_1$ . The image of the exit slit of *T* in the pupil plane has

dimensions, height 0.5 mm., width 0.4 mm. approximately. A rotating shutter in the test stimulus beam exposes the latter for 0.2 sec. once in 3 sec., and also operates a warning buzzer which sounds 0.5 sec. before and 0.1 sec. after each exposure. The second 2 in. beam-splitter cube  $C_2$

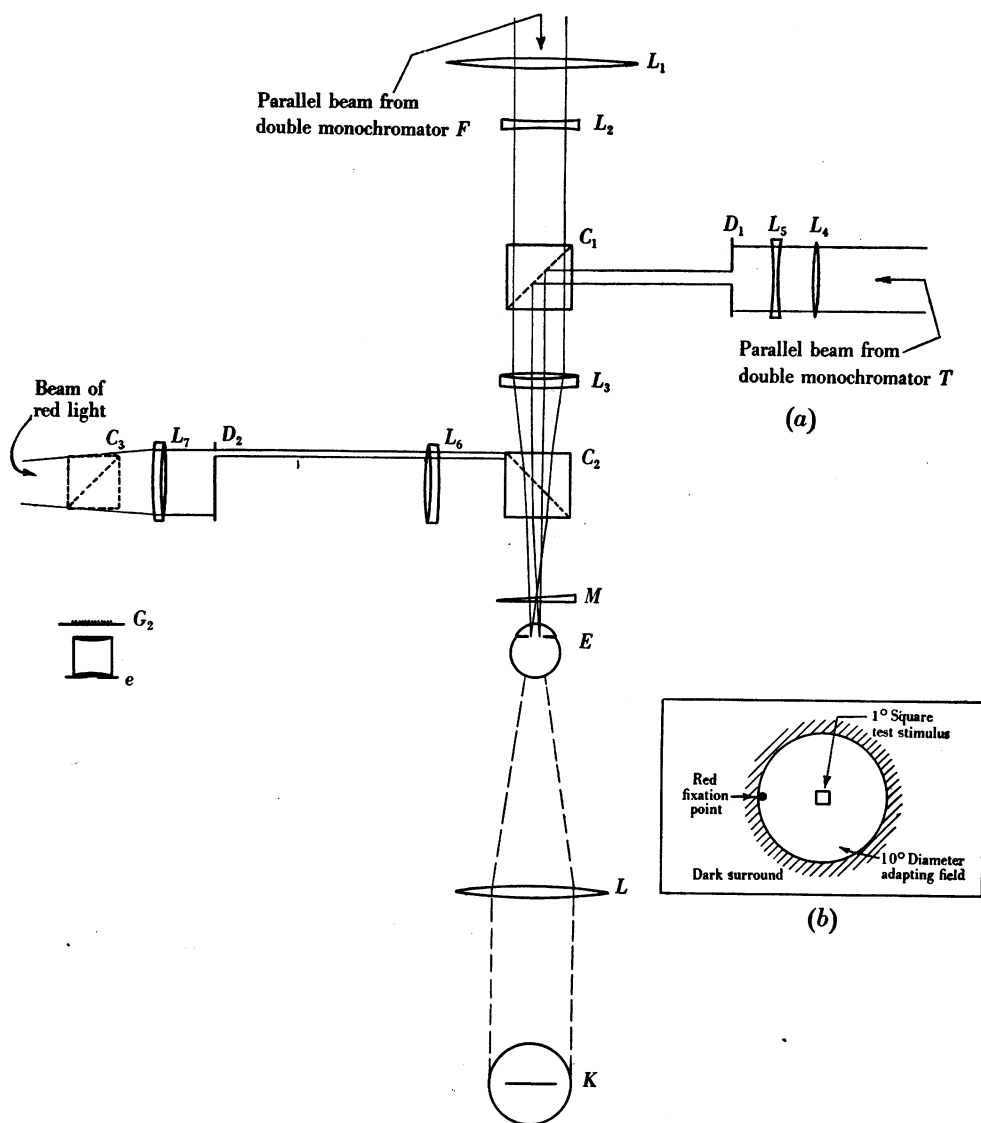


Fig. 1. (a) Plan of apparatus (not to scale). (b) Observational field as seen by the subject.

introduces the fixation field of deep red, filtered light, again focused in the plane of the pupil. A diaphragm  $D_2$  in the focal plane of lens  $L_6$  limits the beam to the required fixation pattern which in the present work consists of a single small patch a few minutes in diameter placed 5° to the left of the test stimulus. Fig. 1(b) shows the field as seen by the subject.

The subject's head is kept rigidly fixed with respect to the apparatus by requiring him to bite on a dental impression formed in sealing-wax on a brass base-plate carried by a massive lathe slide-rest equipped with adjustments in three directions and clamped to the table. The head is brought to the correct position in the following way. Lens  $L_1$  is first moved to its standard 'zero' adjustment and a concentric ring graticule  $G_1$  is set up in the eye position with its centre coincident with the image of the exit slit of  $F$ . Diaphragm  $D_2$  is removed, the cube  $C_2$  is inserted and the image of the graticule  $G_1$  formed by the lenses  $L_6$  and  $L_7$  after reflexion in  $C_2$  is observed with an eyepiece  $e$ . A second graticule  $G_2$  in the focal plane of  $e$  is adjusted to be concentric with the image of  $G_1$ .  $G_1$  is then removed and a small opal lamp is placed in the parallel beam from  $F$  at approximately the focal point of  $L_2$ . When the subject bites on his dental impression and looks at the correct part of the field,\* an image of the opal lamp is formed by reflexion at the cornea and the rays from this image after reflexion in  $C_2$  are focused at or near the graticule  $G_2$ . By means of the three adjustments on the slide rest the subject's head is moved until the image of the opal lamp as seen in  $e$  appears in focus at the centre of  $G_2$ . With the head in this position, the beam of the adapting field enters the eye at a known reference point and any other point of entry can be obtained by displacing lens  $L_1$  by a measured amount.

To specify point of entry and hence angle of incidence on the retina for vision at any retinal point  $P$  the following convention will be used. Consider the bundle of all rays outside the eye which after refraction in the eye terminate on  $P$ . This bundle will not generally be parallel but for an emmetropic eye with relaxed accommodation and for points  $P$  at or near the fovea it will be approximately so. Some ray in the bundle, produced forward without refraction, will pass through the principal corneal reflex (c.r.) point, i.e. the point occupied by the virtual image formed by corneal reflexion, of a distant source on the visual axis. Take a plane normal to this ray through the principal c.r. point. The point of entry for any ray in the bundle is specified by the position of its intercept with this plane. Rays of different wave-lengths incident on  $P$  in the same direction have slightly different points of entry but the differences are negligible for the present work. The c.r. point used in adjusting the eye is displaced laterally from the principal c.r. point by approximately  $0.34 = 5/57.3 \times 7.8/2$  mm. (7.8 mm. = radius of curvature of the cornea), because the subject's visual axis is directed  $5^\circ$  to the left of the distant source.

The weak prism ( $M$ ) (10 prism diopters) deflects the whole field presented to the subject by  $5.7^\circ$  to the right side and allows him to sit squarely to the apparatus and see the fixation point directly ahead.

The intensities of the stimuli entering the eye were measured by removing the prism  $M$  (for which an allowance was made) and imaging the central area of the  $10^\circ$  field on the sensitive surface of a KMV6 photocell  $K$ . This photocell formed the receptor unit of a photoelectric photometer calibrated to give absolute energy intensities throughout the visible spectrum.

The unit in which the intensities of all stimuli (including threshold stimuli) referred to in this paper are expressed is as follows: 1 erg per sec. entering the eye per square degree of field. To convert to luxons (photons), the values must be multiplied by  $2.18 \times 10^6 V_\lambda$ , where  $V_\lambda$  is the C.I.E. relative luminosity factor for the wave-length in question. The overall width of the spectrum band used varied with wave-length from 4.1 to 23.3 m $\mu$ . (adapting field) and from 4.5 to 26.7 m $\mu$ . (test stimulus), over the spectrum range 425–700 m $\mu$ . In deriving the spectral sensitivities given on p. 198, slit width corrections (only appreciable in the red) were applied.

In determining a threshold value for the test stimulus, under prescribed conditions, the subject first made an approximate setting by varying a neutral wedge in the test stimulus beam. A set of five exposures at nine intensities, centred on the approximate value and separated by steps of 0.07 log unit, was then given, in random order, together with ten blank exposures. The subject's response 'seen' or 'not seen' to each exposure was recorded and a rough frequency of seeing curve constructed, from which the final threshold was read off as the intensity corresponding to 50 %

\* As diaphragm  $D_2$  is removed, the fixation point is not visible but accurate fixation is not necessary for the present purpose.

seeing chance. About 1 hr. before each set of measurements the pupil of the subject's observing eye was dilated with euphthalmine hydrochloride. The subject then remained in complete darkness until observations were commenced.

Four subjects were used:

Subject	Age (yr.)		
F.F.	32	Right eye	Hypermetrope +1.5 sph.
K.H.S.	25	Right eye	Emmetrope —
W.S.S.	45	Left eye	Hypermetrope +0.5 sph.
R.G.B.	19	Right eye	Emmetrope —

## RESULTS

### *Measurements on a field of zero brightness*

*Pupil traverses.* The variation of the  $5^\circ$  parafoveal threshold  $U_\lambda$  of the fully dark-adapted retina when the point of entry of the test stimulus was traversed across a horizontal chord of the pupil through the principal c.r. point, is shown

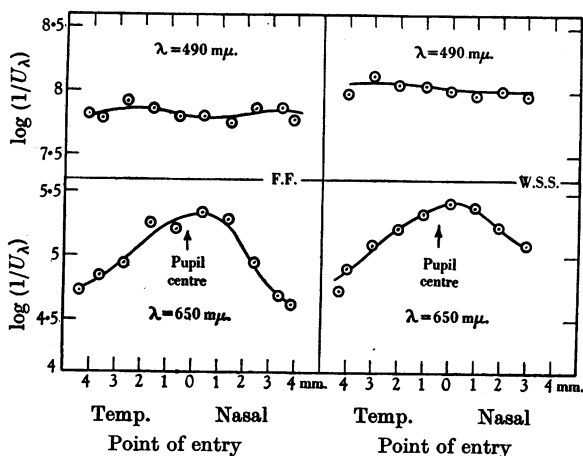


Fig. 2.

Fig. 2. Variation of the  $5^\circ$  parafoveal threshold on a dark field for wave-lengths 490 and 650  $\text{m}\mu$ . as the point of entry of the test stimulus beam is traversed across the pupil. Subjects: F.F. and W.S.S.

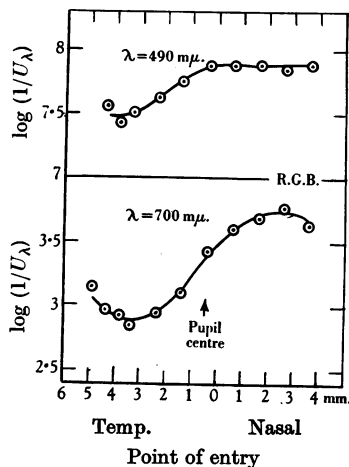


Fig. 3.

Fig. 3. As for Fig. 2. Subject: R.G.B.

in Fig. 2 for subjects F.F. and W.S.S. and for test stimuli of wave-lengths 490 and 650  $\text{m}\mu$ . The quantity plotted is log sensitivity, i.e.  $\log (1/U_\lambda)$ . For these subjects, there is approximate constancy of the sensitivity for  $\lambda = 490 \text{ m}\mu$ . and for  $\lambda = 650 \text{ m}\mu$ ., a well-marked directional effect with maximum sensitivity when the beam enters near the pupil centre. For subject R.G.B., on the other hand, it was found (a) that maximum sensitivity for a red test stimulus occurred when the stimulus entered near the nasal edge of the pupil, (b) that for the blue-green test stimulus, the sensitivity, while approximately constant

in the nasal half of the pupil, dropped significantly in the temporal half (Fig. 3). Some difficulty was experienced in obtaining satisfactory measurements for this subject. The curves of Fig. 3 are two of several traverses all of which showed the features just noted. The rise in sensitivity near the temporal edge which appears in the curves of Fig. 3 is less certain. The fact that for some eyes the maximum sensitivity may occur for points of entry considerably displaced from the pupil centre has been noted before (Flamant, 1946; Stiles, 1939). Such displacements probably arise from a shearing-over of the retinal end-organs so that their axes are not pointing at the pupil centre. For R.G.B. this may well have occurred without any change in other threshold properties. His maximum sensitivity for  $\lambda=490\text{ m}\mu$ . is about the same in absolute magnitude as the mean for F.F. and W.S.S. and other measurements show that at 650 and 700  $\text{m}\mu$ . it is only about 0.1–0.2 log units lower than the corresponding means for these subjects. Moreover, if one imagines R.G.B.'s pupil displaced about 3 mm. to the nasal side to bring the maximum sensitivity for 700  $\text{m}\mu$ . to the pupil centre, most of the anomalous temporal halves of the curves of Fig. 3 would be inaccessible to observation and, assuming symmetry of the curves about the maximum, the results would agree substantially with those of other subjects. The results for R.G.B. may show in fact what would be obtained with subjects generally if the angle of incidence on the retina could be varied outside the limits normally set by the pupil.

The maximum sensitivity on the horizontal chord through the principal c.r. point is not necessarily the absolute maximum, which may occur at a point above, or below the chord. Vertical traverses indicated that for F.F., W.S.S. and R.G.B. the point of absolute maximum sensitivity was not displaced from the horizontal chord by more than about 1.5 mm. For the subsequent measurements attention was confined to two points of entry, both on the horizontal chord, one at the position of maximum sensitivity, the other as far from this position as permitted by the pupil. These positions, referred to as *central* and *peripheral entry* respectively are shown in Table 1.

TABLE 1

Subject	Points of entry used, mm. nasal (N.) or temporal (T.)	
	Central entry	Peripheral entry
F.F.	0.6 T.	3.3 N.
	(later) 0.3 T.	4.1 T.
K.H.S.	0.3 T.	3.8 T.
W.S.S.	0.2 T.	3.2 T.
R.G.B.	2.4 N.	3.6 T.

The choice of positions for K.H.S., for whom no traverses were made, assumed that his maximum sensitivity occurred approximately at the pupil centre.

*Two-point comparisons.* Using the ratio of the threshold for peripheral and central entry as a measure of the directional sensitivity of the retina, the observations plotted in Fig. 4 show how the directional effect varies with the wave-length of the test stimulus. For the first three subjects the directional

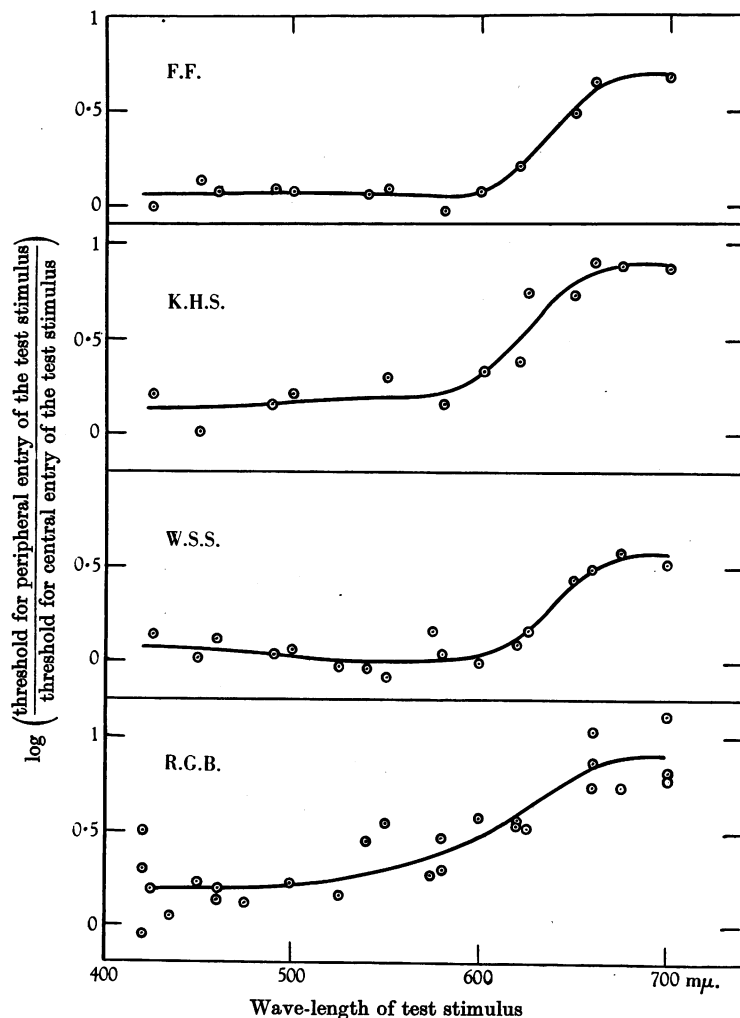


Fig. 4. Ratio of the 5° parafoveal thresholds for peripheral and central entry of the test stimulus in the pupil, for various wave-lengths of the test stimulus. Zero adapting field. Four subjects.

effect is slight and nearly constant for  $\lambda < 600 m\mu$ , but between 600 and 670  $m\mu$ . it increases by 0.6–0.7 log units (4 or 5 to 1). For R.G.B. more results were obtained because of the wide spread in his observations. It seems probable that for this subject there is a significant rise in directional sensitivity in the range below 600  $m\mu$ . as well as a marked increase at longer wave-lengths.

Subjects were asked to report on the apparent colour of the test stimulus when it was just above the threshold. The reports were fairly consistent in showing (a) that for wave-lengths below about 600 m $\mu$ . the test stimulus appeared white for both points of entry, (b) that as  $\lambda$  was increased from 600 to 700 m $\mu$ . the test stimulus appeared coloured (orange or red) for central entry and white for peripheral entry.

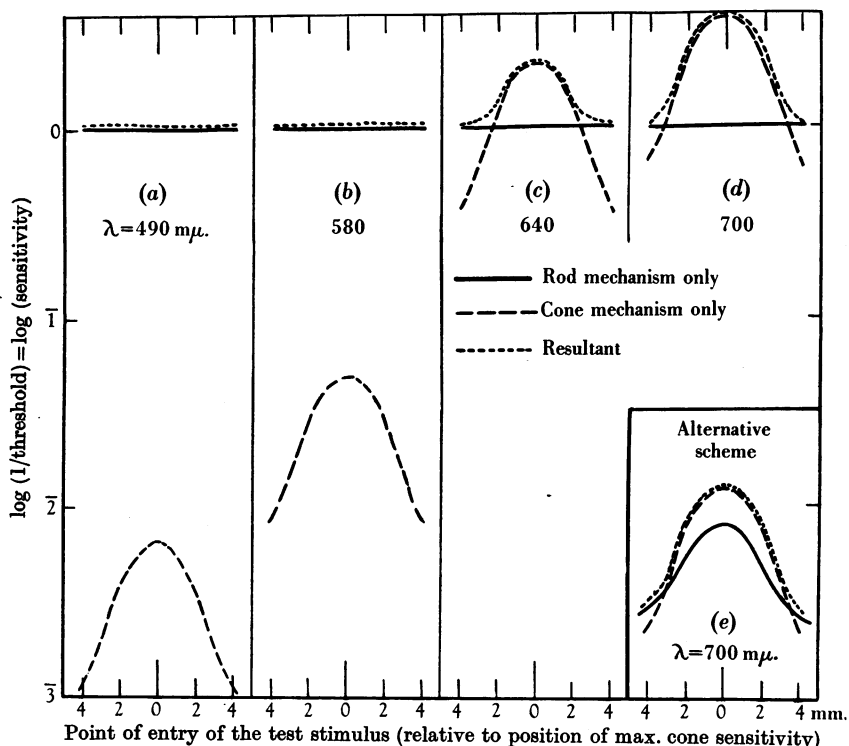


Fig. 5. Diagram illustrating how the observed variation of threshold with point of entry of the test stimulus may be explained in terms of a non-directional rod and a directional cone mechanism. The rod sensitivity is taken as unity at all wave-lengths.

In the parafovea both rod and cone mechanisms are operative and with each may be associated a threshold value which would be observed if the other mechanism were out of action, the threshold actually observed under any particular conditions being equal to the smaller of the two. The results just given are consistent with the view that, for all wave-lengths, the threshold of the rod mechanism is nearly independent of point of entry (at least within a range of 3-4 mm. from the central position) while for the cone mechanism the threshold has a pronounced minimum for central entry. The variation of observed threshold with point of entry for different wave-lengths would then arise in the way indicated in Fig. 5 (a) to (d) ( $\log(\text{sensitivity}) = \log(1/\text{threshold})$ ).



is plotted). Two points may be noted. Since, for peripheral entry, even a deep red stimulus is seen as white at the threshold it seems that cone sensitivity never sufficiently exceeds rod sensitivity completely to take over vision of the test stimulus at the threshold. The results for subject R.G.B. show that for him (and possibly for other subjects) (a) the constancy of the rod threshold is not maintained as the point of entry is moved to 6 mm. from the central position, and (b) the deviation from constancy increases with wave-length in the range below 600  $m\mu$ . where cone vision is not a factor.

The experimental results so far given would not exclude the alternative possibility that the rods develop a marked directional effect as  $\lambda$  increases beyond 600  $m\mu$ ., so that for example at  $\lambda = 700 m\mu$ . the scheme of Fig. 5 (e) would apply instead of Fig. 5 (d). Determinations of the directional sensitivity by the indirect method described above make this alternative improbable.

#### *Adapting field illuminated*

In applying the indirect method it is inconvenient to vary the intensity of the adapting field so that it raises the threshold by an exactly prescribed factor. Instead, the adapting field was set at a fixed intensity known from preliminary tests to raise the threshold for a test stimulus of wave-length 490  $m\mu$ . by a factor which varied in different runs from about 0.7–1.3 log units. The threshold for the 490  $m\mu$ . test stimulus was then measured for central and peripheral entry of the field, the test stimulus being always sent in through the central position. If for each of the two points of entry the threshold were strictly proportional to the intensity of the adapting field (Weber's law strictly true), the ratio of the two thresholds measured in this way would be identical with the ratio of the adapting field intensities for peripheral and central entry necessary to raise the threshold by precisely the same factor. Although Weber's law is a poor approximation under the conditions of the present experiments, the ratio of the observed threshold can still be used as a measure of the directional property. The further interpretation of this measure is deferred until after the experimental results have been given.

In Fig. 6 the logarithm of the ratio of the thresholds for central and peripheral entry of the adapting field is plotted against the wave-length of the latter (plotted points and continuous curves). The ratio central/peripheral is used in this case instead of peripheral/central (Fig. 4) since a high sensitivity to the adapting field corresponds to a high threshold value. Comparing the curves of Figs. 4 and 6, the outstanding difference is the absence of the marked increase in directional effect when  $\mu$  exceeds 600  $m\mu$ . For the first three subjects, the directional sensitivity to the adapting effect of the field is small and nearly constant throughout the spectrum. For R.G.B. there is a rather larger directional effect, which increases with wave-length but the high values previously obtained in the red do not appear.

Although the adapting fields of different wave-lengths were set to raise the threshold for 490  $m\mu$ . by about the same factor, the field appeared much brighter as the red end of the spectrum was approached. Moreover in the red the apparent brightness increased materially when the point of entry was changed from the centre to the edge, despite the fact that the effect on the threshold for 490  $m\mu$ . was practically the same (except for subject R.G.B.).

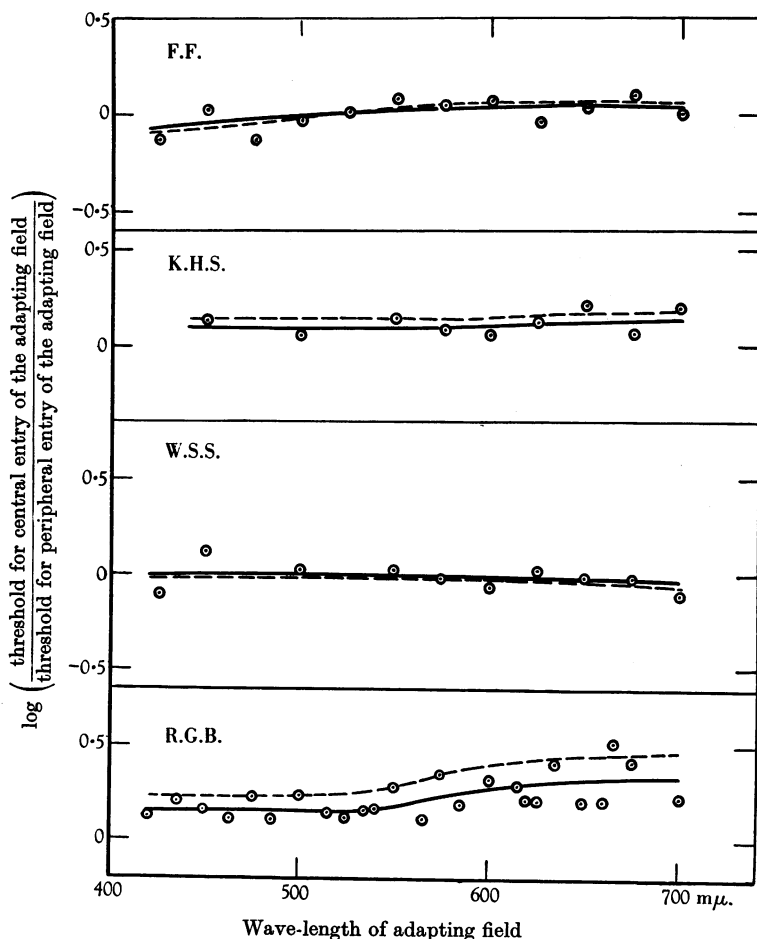


Fig. 6. Ratio of the 5° parafoveal thresholds for central and peripheral entry of the adapting field in the pupil, for various wave-lengths of the adapting field. Test stimulus of fixed wave-length (490  $m\mu$ .) and fixed point of entry (central) throughout.

The curve of Fig. 7 (taken from Stiles, 1939) shows how the threshold for a test stimulus seen by parafoveal rod vision increases as the intensity of the adapting field is raised. It was obtained under conditions which were the same as those used in the present work except that the test stimulus was exposed in

flashes of 0.063 sec. instead of 0.2 sec. By convention, the units of test stimulus and field intensity in Fig. 7 are so chosen that the threshold for zero field, and the field intensity to raise the threshold by the factor 10, both have the value 1. The range of the present measurements corresponds to the shaded stretch of the curve of Fig. 7 where the mean gradient,  $d \log (\text{threshold})/d \log (\text{field})$ , equals 0.7 as against the value 1 which would mean obedience to Weber's Law. The log ratios of the thresholds in Fig. 6 should therefore be increased by

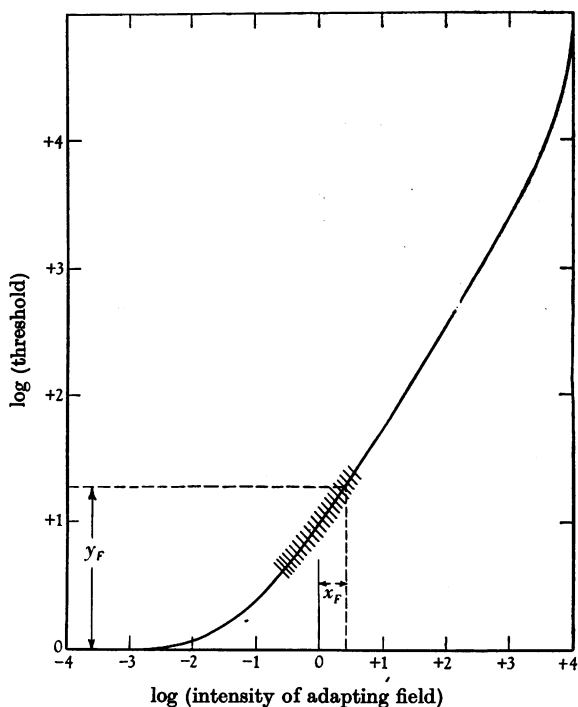


Fig. 7. Variation of the threshold of the parafoveal rod mechanism with the intensity of the adapting field (Stiles, 1939). The range involved in the present measurements is shown shaded.

a factor of on the average  $1/0.7$  to obtain the correct measure of the directional sensitivity to the adapting effect of the field. This correction has been made in Fig. 6, where the broken curves are derived from the continuous curves by multiplying the ordinates by  $1/0.7$ .

It may be concluded that within 3–4 mm. of the central position the rod mechanism is nearly non-directional in its response to an adapting field for all wave-lengths of the latter. It is highly probable therefore that the rod response to a test stimulus is also non-directional throughout the spectrum, as it certainly is for  $\lambda$  below  $600 \text{ m}\mu.$ , and the scheme of Fig. 5 (*d*) must be accepted in preference to that of Fig. 5 (*e*).

For subject R.G.B., comparison of the curve of Fig. 4 with the broken curve of Fig. 6 in the range below 600 m $\mu$ . indicates that the deviations from non-directionality which the rod mechanism shows at 6 mm. from the central position are similar for test stimulus and adapting field.

### *Spectral sensitivity curves*

As all the thresholds and field intensities were measured in energy units, certain spectral sensitivity curves can be derived from the results. For the measurements with zero field, the mean values of  $\log(1/\text{threshold})$ , i.e.  $\log(\text{sensitivity})$ , at the wave-lengths for which observations were made on all four subjects, are given in columns 2 and 3 of Table 2. The  $\log(\text{sensitivity})$  to the adapting effect of the field (columns 5 and 6) was obtained in the following way. Suppose  $(U_{490})_0$  is the measured threshold on zero field and  $(U_{490})_F$  is the value on an adapting field of wave-length  $\mu$  and intensity  $W_\mu$ . The increase in  $\log(\text{threshold})$  produced by the field is

$$y_F = (\log U_{490})_F - (\log U_{490})_0$$

and according to the curve of Fig. 7 this corresponds to a field intensity exceeding by  $x_F$  log units that required to raise the threshold by the factor 10. The latter intensity, or rather its logarithm, is therefore  $(\log W_\mu - x_F)$  and the corresponding  $\log(\text{sensitivity})$  is  $(x_F - \log W_\mu)$ . This procedure assumes that the rod curve of Fig. 7 (determined by Stiles (1939) for subject W.S.S.) has the same *shape* for all the subjects, at least over the shaded range. The parafoveal threshold measurements by Hecht, Peskin & Patt (1938) and measurements on other subjects in this laboratory show that the shape of the curve varies very little from one subject to another so that no material error is expected from this assumption.

TABLE 2. Mean spectral sensitivities for 5° parafoveal vision

Log (sensitivity to the test stimulus) $\log(1/U_\lambda)$			Log (sensitivity to the adapting field) $x_F - \log W_\mu$		
			(Derived from measurements with a test stimulus of wave-length 490 m $\mu$ .)		
Wave-length of test stimulus	Central entry	Peripheral entry	Wave-length of adapting field	Central entry	Peripheral entry
425	7.06	6.95	450	6.40	6.26
450	7.58	7.48	500	6.80	6.72
500	8.02	7.83	550	6.60	6.42
550	7.84	7.62	575	6.14	5.98
580	7.15	7.01	600	5.42	5.29
620	6.15	5.85	625	4.70	4.60
650	5.44	4.84	650	3.85	3.70
660	5.30	4.55	675	3.06	2.98
700	4.02	3.27	700	2.26	2.07
Additive constant to bring maximum sensitivity to unity	- 8.06	- 7.87		- 6.84	- 6.76

In plotting the four spectral sensitivity curves of Table 2, the maxima have been brought to the value unity by adding to the log values an appropriate constant which is also shown in Table 2. From the measurements of the

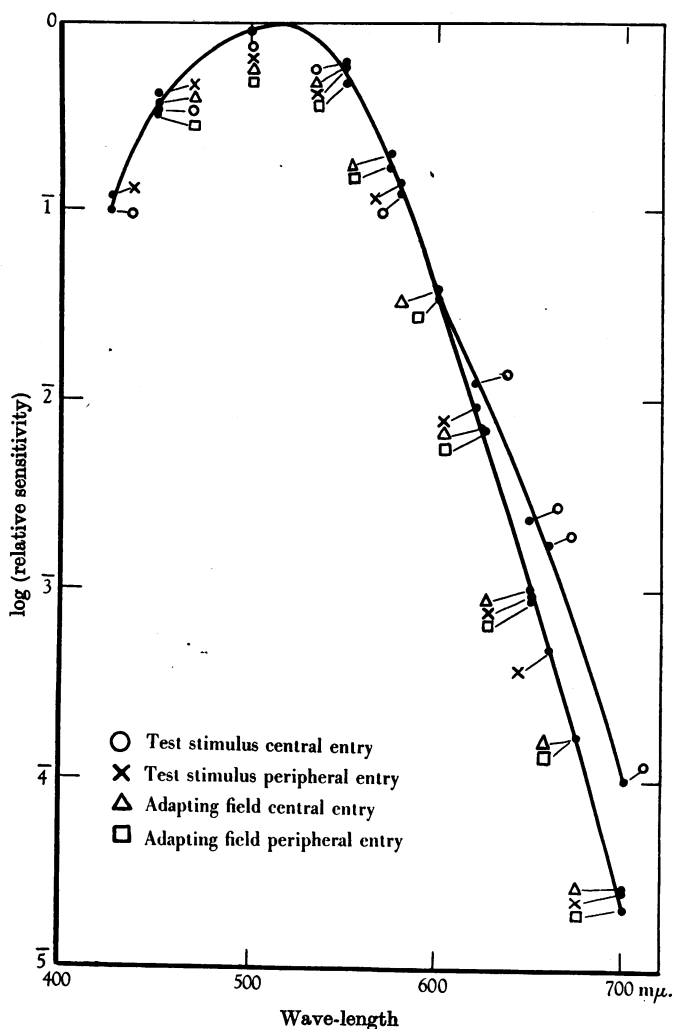


Fig. 8. The relative spectral sensitivity of the 5° parafoveal retina determined from the thresholds on zero field for central and peripheral entry of the test stimulus, and from the intensities of adapting fields, entering centrally and peripherally, which raise the threshold by a given factor.

directional effect already given it is clear that to a first approximation the test stimulus sensitivity curves ( $\circ$  and  $\times$  in Fig. 8) must agree for  $\lambda < 600 \text{ m}\mu$ . and then separate, while the adapting field sensitivity curves ( $\triangle$  and  $\square$ ) must agree over the whole spectrum. It is now seen (a) that for  $\lambda < 600 \text{ m}\mu$ . all four curves

agree, (b) that for  $\lambda > 600 \text{ m}\mu$ . the adapting field curves agree with the test stimulus curve for peripheral entry. From (a), it follows that the relative spectral sensitivity of the rod mechanism is the same whether derived from the adapting effect or from the absolute threshold. Result (b) supports the view that the absolute threshold for peripheral entry of the test stimulus corresponds to rod vision, in the red as well as over the rest of the spectrum.

The recent measurements of the  $8^\circ$  parafoveal threshold by Wald (1945) were made with the natural pupil but from the existence of a photochromatic interval even in the red, Wald is able to conclude that the results refer to rod vision throughout. Compared with Wald's results, the present rod sensitivity curve (mean for  $\times$ ,  $\Delta$  and  $\square$  points in Fig. 8) is rather higher in the red (Table 3). Apart from a possible difference because of the difference in parafoveal angle, Wald's results based on twenty-two subjects are no doubt closer to a representative mean rod curve than the present ones based on four subjects.

TABLE 3. Log (relative rod sensitivity)

Wave-length	365	405	436	492	546	578	621	691	713	750
Wald	5.71	2.10	1.35	1.97	1.77	1.05	3.71	5.31	6.46	7.56
Read from mean curve ( $\times$ , $\Delta$ , $\square$ ) Fig. 8	—	—	1.30	1.94	1.78	1.15	3.94	5.62	—	—

#### *Change in directional sensitivity with adaptation level*

This has been considered at some length in Stiles, 1939, but the following measurements on one subject F.F. for a case not discussed in that paper are of interest. Fig. 9 shows the variation with field intensity of the threshold for a test stimulus of wave-length  $\lambda = 640 \text{ m}\mu$ ., seen by  $5^\circ$  parafoveal vision on an adapting field of wave-length  $\mu = 490 \text{ m}\mu$ . (a) for central entry, (b) for peripheral entry of the test stimulus. The adapting field entered centrally throughout. The curves can be interpreted in the following way. At zero field, the situation corresponds to Fig. 5(c), the test stimulus being seen respectively by cone and rod vision for central and peripheral entry. Because the sensitivity of the rod mechanism to wave-length  $490 \text{ m}\mu$ . is much greater than that of the cone mechanism, the first result of increasing the field intensity is to raise the rod threshold leaving the cone threshold unchanged, or nearly so. Thus the threshold for peripheral entry is raised until the rod threshold exceeds the cone threshold, it then remains constant until the field is sufficiently intense to begin raising the cone threshold. At this intensity the threshold for central entry should start to increase. On the whole the results fit this interpretation satisfactorily.

#### *Precision of the threshold*

The measured thresholds were all derived from rough frequency of seeing curves. The slope of the frequency of seeing curve at the 50 % value is a measure of the intrinsic sharpness or precision of the threshold, which must be regarded

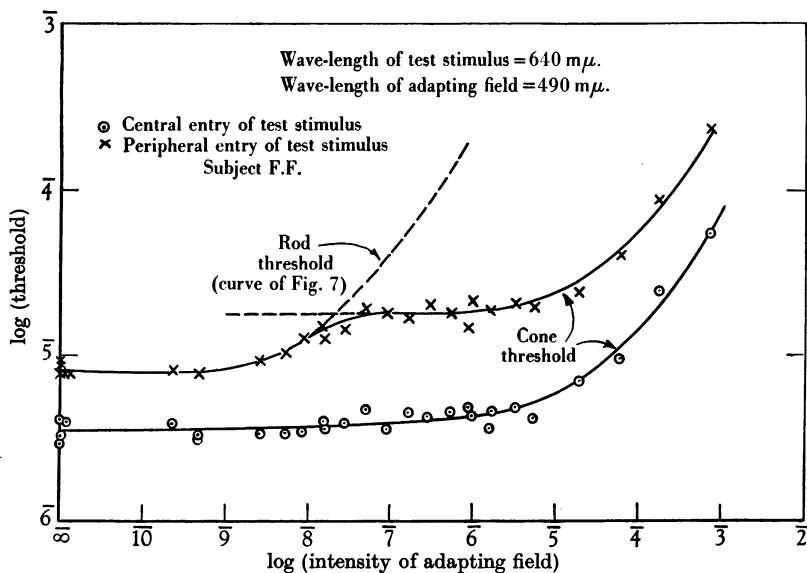


Fig. 9. Curves showing (a) the transition from rod to cone vision of the test stimulus when the latter enters the pupil peripherally, (b) the absence of any marked transition for central entry of the test stimulus.

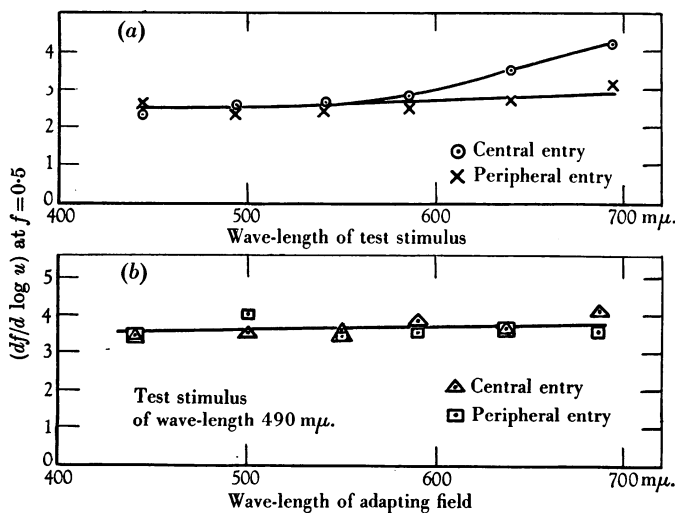


Fig. 10. Precision of the threshold. Slope  $(df/d \log u)$  of the frequency-of-seeing curve at the 50% point, for observations (a) on zero field with central or peripheral entry of the test stimulus, (b) on an adapting field entering centrally or peripherally.

as arising both from biological fluctuations of the visual mechanism and from quantum fluctuations of the test stimulus. This slope is given by  $df/d \log u$  at  $f=0.5$ , where  $f$  is the proportion of 'seen' response to a test stimulus of intensity  $u$ . The mean slopes for all the observations of the four subjects under the four principal conditions are plotted in Fig. 10. For test stimuli presented on zero field (Fig. 10 (a)) the observed precision in the red is slightly higher for central than for peripheral entry, a difference associated perhaps with a greater sharpness of the cone compared with the rod threshold. When the adapting field is applied the precision of the threshold for the test stimulus of fixed wave-lengths  $490 \text{ m}\mu$ . is independent of the wave-length and the point of entry of the field (Fig. 10 (b)) but is rather higher than for zero field (3.5 compared with 2.5).

#### SUMMARY

1. The absolute parafoveal threshold for a monochromatic test stimulus is nearly independent of the angle of incidence of the light on the retina for wave-lengths below  $600 \text{ m}\mu$ ., but exhibits a marked directional effect in the red. It does not follow that the response of the parafoveal rod mechanism becomes directional in the red, because in this spectral region cone vision, which is highly directional, may be participating.

2. By determining the extent to which the threshold for a blue test stimulus ( $\lambda=490 \text{ m}\mu$ .) is raised by adapting fields of different wave-lengths, incident on the retina at different angles, it is shown that the rod response to an adapting field is non-directional, or nearly so, for all colours of the field.

3. It is also shown that the relative spectral sensitivity of the rod mechanism is the same whether determined by the direct threshold method or indirectly from the adapting effect of the field.

4. For one subject, the measurements indicate that the retinal end-organs, in the parafoveal area used, point towards the edge rather than towards the centre of the pupil. His results suggest that the rods may show a directional response when the retinal angle of incidence can be increased beyond the limit normally set by the pupil.

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